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Soft-bottom mollusc assemblages in the Ría de Ares-Betanzos (Galicia, NW Spain)

Asociaciones malacológicas de substratos blandos de la Ría de Ares-Betanzos (Galicia, NO España)

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ABSTRACT

The composition and spatial distribution of the mollusc fauna on the subtidal soft bottoms of the Ría de Ares-Betanzos (Galicia, NW Spain) were studied by means of semi-quantitative sampling and multivariate analyses. The faunal distribution in the ría seems to be mainly conditioned by a depth and grain size gradients, the latter defined by a increase in silt/clay and a decrease of coarser granulometric fractions from the mouth towards the margins and inner areas of the ría. Several assemblages were determined which could be defined according to the classic terms of 'community' and 'facies'. Sandy bottoms showed a '*Venus fasciata* community' in coarser sediments of the outer ría, while a '*Venus gallina* community' was found in fine sand at the center of the ría. The shallower and muddier sediments in the inner ría showed a mix of typical species from the '*Abra alba*' and the '*Venus gallina*' communities. However, two facies could be distinguished: the 'facies of *Ringicula auriculata-Pandora inaequivalvis*' in sediments with a greater fine sand content, and the 'facies of *Nassarius pygmaeus-Dentalium novemcostatum*' in the muddiest sediments.

RESUMEN

Se estudia la distribución espacial de los Moluscos en los fondos blandos de la Ría de Ares y Betanzos (Galicia, NO, España) utilizando muestras semi-cuantitativas y técnicas de análisis multivariante. La distribución de la fauna parece estar condicionada principalmente por la profundidad y por los gradientes en el tamaño de grano, definidos por un incremento de la fracción pelítica y una disminución de las fracciones gruesas de sedimento desde la boca hasta los márgenes y zonas internas de la ría. Las agrupaciones halladas pueden ser definidas dentro de los términos clásicos de 'comunidades' y 'facies'. Los fondos de arena en la parte más externa de la ría donde los sedimentos son más gruesos presentan la 'comunidad de *Venus fasciata*', mientras que la 'comunidad de *Venus gallina*' fue encontrada en fondos de arena fina en la parte central de la ría. Los fondos fangosos se encuentran en zonas más someras del interior de la ría y presentan una mezcla de especies típicas de las comunidades de '*Abra alba*' y '*Venus gallina*'. Sin embargo dos facies pueden ser distinguidas: la 'facies de *Ringicula auriculata-Pandora inaequivalvis*' en sedimentos con altos contenidos de arenas finas y la 'facies de *Nassarius pygmaeus-Dentalium novemcostatum*' en los sedimentos más fangosos.

KEY WORDS: Soft-bottom, molluscs, distribution, Ría de Ares-Betanzos.
PALABRAS CLAVE: Substratos blandos, moluscos, distribución, Ría de Ares-Betanzos.

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INTRODUCTION

During the last thirty years, there has been an ongoing interest in the 'rías' of Galicia (NW Spain), which are a special kind of estuarine system. The rías originated from flooded river valleys and have a high primary productivity due to upwellings and regular inflows of nutrients (NOMBELA, VILAS AND EVANS, 1995). The great economic and social importance of these systems (fisheries, bivalve culture on rafts, shellfish resources) would greatly benefit from a scientific study of the environment, especially that of the benthic communities, which are good indicators of the conditions of marine bottoms (BELLAN, 1967; PEARSON AND ROSENBERG, 1978; WARWICK, 1988).

The Ría de Ares-Betanzos is the largest ría of north-west Galicia and is located between the Ría de Coruña and the Ría de Ferrol (Golfo Ártabro). This ría is a double estuarine system with depths ranging between 2 and 43 m (SÁNCHEZ-MATA, GLÉMAREC AND MORA, 1999). Over the last years, several papers have been devoted to its benthic macrofauna (SÁNCHEZ-MATA, MORA, GARMENDIA AND LASTRA, 1993; TRONCOSO AND URGORRI, 1993a; GARMENDIA, SÁNCHEZ-MATA AND MORA, 1998; SÁNCHEZ-MATA AND MORA, 1999a; b). Furthermore, the hard-bottom mollusc fauna was studied by TRONCOSO, URGORRI, PARAPAR AND LASTRA (1988) and TRONCOSO, URGORRI AND OLABARRÍA (1996) while TRONCOSO AND URGORRI (1992, 1993b) analyzed the vertical distribution of infauna in the sediment. However, there is a lack of synecological studies on soft-bottom malacofauna. Thus, this paper deals with the distribution of soft-bottom mollusc assemblages and the relation with environmental parameters in the subtidal areas of the Ría de Ares-Betanzos. On the other hand, this area was strongly affected by the Aegean Sea oil spill during 1993, and this paper can therefore serve as a baseline study for future comparisons of molluscan fauna evolution.

MATERIAL AND METHODS

Sample collection: A total of 55 stations were sampled in subtidal soft bottoms to cover adequately the extension of the ría (Fig. 1). Sampling program was carried out between February and November 1986. Semi-quantitative data were obtained using a naturalist rectangular dredge. Sampled area varied between stations depending on nature of substrate; data were standarized to 25 l of collected sediment (maximum volume of dredge net). Samples were sieved through a 0.5 mm mesh; fauna was sorted in the laboratory after fixation in 10% buffered formalin. An additional sediment sample was taken at each station to analyze the granulometric composition, carbonates, nitrogen (N), organic carbon (C) and total organic matter (TOM) contents (TRONCOSO AND URGORRI, 1993a). The following granulometric fractions were considered: gravel (GR, >2 mm), coarse sand (CS, 2-0.5 mm), medium sand (MS, 0.5-0.25 mm), fine sand (FS, 0.25-0.063 mm), and silt/clay (<0.063 mm). Median grain size (Q50), sorting coefficient (So) (Trask, 1932) and C/N ratio were also determined for each sample. Sedimentary types were characterized according to RODRIGUES AND QUINTINO (1985) and JUNOY AND VIÉITEZ (1989).

Data analyses: Total abundance of individuals (N) and number of species (S) were calculated for each sampling station. Mollusc assemblages were determined through non-parametric multivariate techniques as described by FIELD, CLARKE AND WARWICK (1982) using the PRIMER v5.0 (Plymouth Routines in Multivariate Ecological Research) software package (CLARKE AND WARWICK, 1994). A similarity matrix between sampling stations was constructed by means of the Bray-Curtis similarity coefficient by first applying square root transformation on species abundance to down-weight the contribution of the most abundant species. From this matrix, a classification of the stations was performed by cluster analysis based on the group-average sorting algorithm, as well

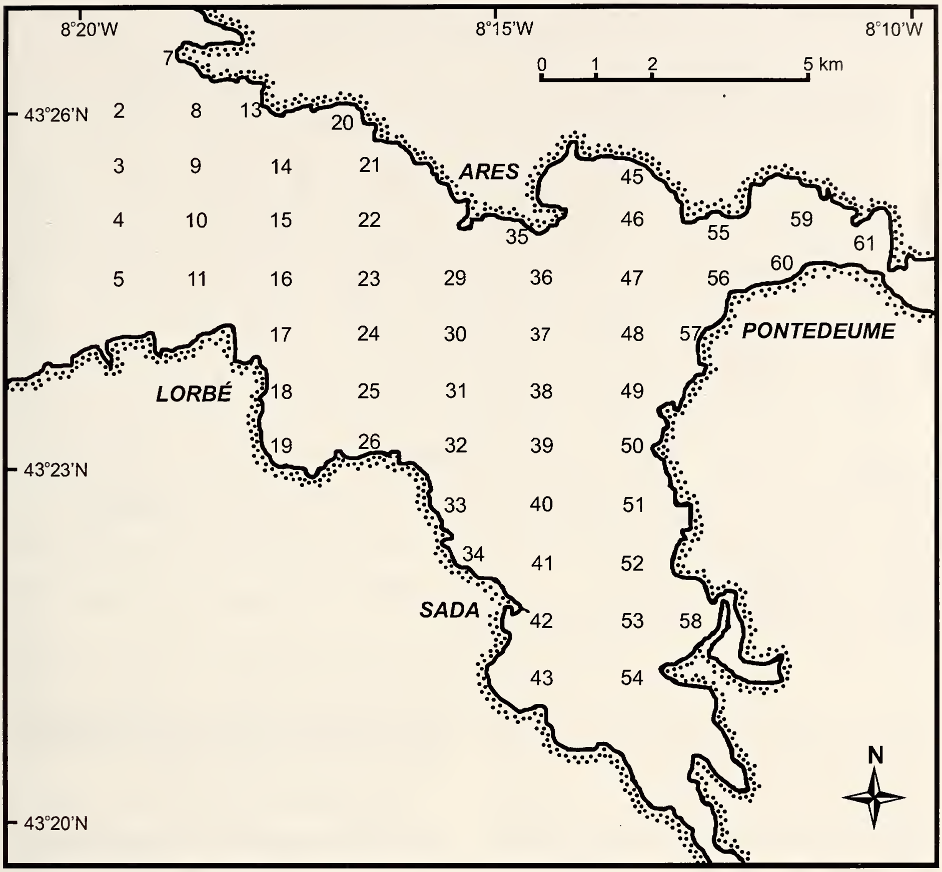

Figure 1. Locations of sampling stations in the Ría de Ares-Betanzos.
Figura 1. Localización de las estaciones de muestreo en la Ría de Ares-Betanzos.

as an ordination by means of non-metrical multidimensional scaling (MDS). Rare species (i.e., those wich appeared in one station and/or with 1–2 invividuals) were included in the final analyses because preliminary trials showed that their supression did not affect classification and ordination of stations. The SIMPER program was next used to identify species that greatly contributed to similarity in a given group derived from those analyses.

The possible relationship between mollusc distribution and the measured environmental variables were researched using the BIO-ENV procedure (belonging to the PRIMER package) and the canonical correspondence analysis (CCA) using the CANOCO v4.02 (Canonical Community Ordination) package (BRAAK, 1988). Forward selection was employed in the latter to detect which variables explained the most variance in the species data. All variables expressed in percentages were previously transformed by log (x+1) and then normalised. Stations 16, 29 and 60 were discarded because of low sediment quantity.

RESULTS

Sediments were mainly of a sandy nature and muddy bottoms were restricted to inner and sheltered areas.

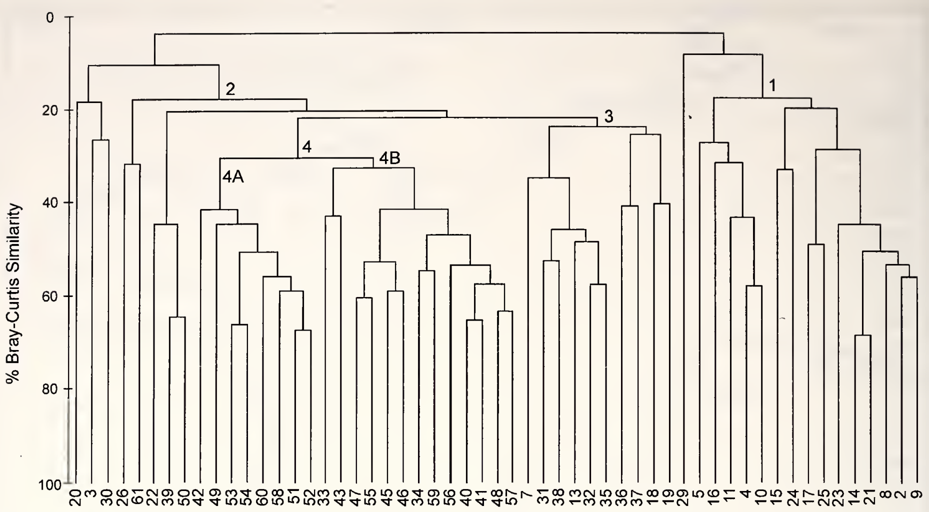

Figure 2. Mollusc assemblages in the Ría de Ares-Betanzos as determined by cluster analysis based on Bray-Curtis similarity coefficient.
Figura 2. Asociaciones malacológicas en la Ría de Ares-Betanzos determinadas por el análisis cluster basado en el coeficiente de similaridad de Bray-Curtis.

Coarser sandy granulometric fractions are greater at the mouth and in the outer areas of the ría and there is a decrease in grain size and an increase in organic content towards the inner areas of the ría (Troncoso and Urgorri, 1993a).

A total of 8030 individuals of molluscs belonging to 116 species were collected, of which 62 were gastropods, 49 bivalves, three polyplacophorans, one scaphopod, and one cephalopod. Gastropods and bivalves were the dominant groups in terms of abundance (48.37 and 46.54%, respectively), followed by scaphopods (4.65%). A complete list of the collected species is provided by Troncoso, Urgorri and Parapar (1993). The gastropods *Nassarius reticulatus* (Linné, 1758), *N. pygmaeus* (Lamarck, 1822) and *Ringicula auriculata* (Ménard, 1811), the bivalves *Chamelea striatula* (da Costa, 1778), *Pandora inaequivalvis* (Linné, 1758) and *Goodallia triangularis* (Montagu, 1803), and the scaphopod *Dentalium novemcostatum* Lamarck, 1818 were the most abundant species in the ría, accounting for 50% of the total mollusc abundance. These species reached their highest abundances in finer sediments excepting *G. triangularis* which prefers coarser sandy sediments (coarse and medium sand).

Multivariate analysis: Cluster analysis and MDS ordination revealed the presence of two large groups of stations at a 12% similarity level (Figs. 2, 3): group 1, comprised sampling stations with coarse sediments (St. 2, 4, 5, 8, 9, 10, 11, 14, 15, 16, 17, 21, 23, 24, 25), and group 2, comprised bottoms of finer granulometry (St. 7, 13, 18, 19, 22, 26, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61). Group 2 could be split into two further groups (25% similarity level): group 3, fine sand bottoms (St. 7, 13, 18, 19, 31, 32, 35, 36, 37, 38), and group 4, sandy bottoms with higher content in silt/clay (St. 33, 34, 40, 41, 42, 43, 45, 46, 47, 48, 49, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60). Furthermore, group 4 could be split in two subgroups (32% similarity level): 4A, which had a greater content of fine sand (St. 42, 49, 51, 52, 53, 54, 58, 60), and 4B, which was comprised of muddier sediments (St. 33, 34, 40, 41, 43, 45, 46, 47, 48, 55, 56, 57, 59). MDS ordination, however, suggests that St. 43 has a greater affinity

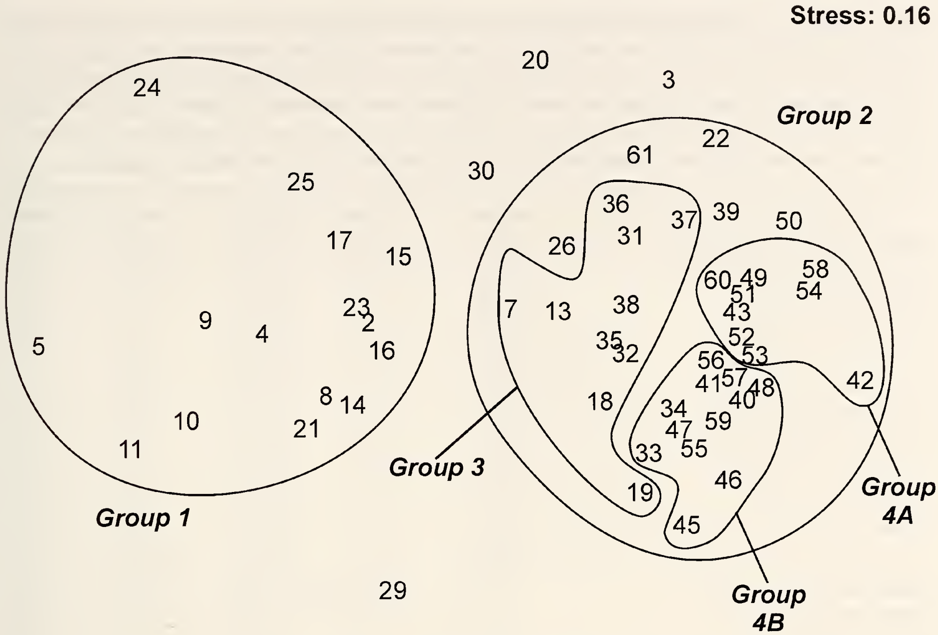

Figure 3. Non-metric multidimensional scaling (MDS) ordination of mollusc assemblages in the Ría de Ares-Betanzos. Groups derived from cluster analysis are delimited by lines.
Figura 3. Ordenación MDS de las asociaciones malacológicas en la Ría de Ares-Betanzos. Los grupos derivados del análisis cluster estan delimitados por líneas.

for subgroup 4A in opposition to that showed in the dendrogram.

MDS ordination also revealed that several sampling points were displaced from the main groupings: St. 3 was a muddy sand basin located in the middle of coarse sands and shows a high abundance of *Acanthocardia paucicostata* (Sowerby, 1841); the samples from St. 20 and St. 30 were very poor in terms of malacofauna; St. 29 had species which are typical of rocky bottoms. On the other hand, St. 22, 39 and 50 appeared displaced from the two main groups within group 2. In addition, St. 26 and 61 show affinities with group 3 but the former is characterized by a dominance of the bivalve *Glycimeris glycimeris* (Linné, 1758) and the latter for the presence of the bivalve *Donax trunculus* Linné, 1758.

Results of the SIMPER analysis are shown in Table I. The bivalves *Goodallia triangularis, Clausinella fasciata* (da Costa, 1778) and *Gari tellinella* (Lamarck, 1818) are the species with a greater contribution to similarity (up to a cumulative 70%) for coarser sandy bottoms of group 1. Group 3 is mainly determined by *Chamelea striatula* and *Nassarius reticulatus*. Group 4A is defined by *Ringicula auriculata, Pandora inaequivalvis, N. reticulatus* and *C. striatula*. Group 4B is characterized by *Nassarius pygmaeus, N. reticulatus, Nucula nitidosa* Winckworth, 1930, *C. striatula, Dentalium novemcostatum, R. auriculata, Corbula gibba* (Olivi, 1792), *P. inaequivalvis* and *Montacuta phascolionis* Dautzenberg and Fisher, 1925.

The BIO-ENV procedure (Table II) showed that the best combinations of environmental variables via the highest correlations with faunistic data was that composed of depth, gravel, fine sand and silt/clay. Depth was the variable with the best value when each variable was considered alone (*pw*: 0.464). The

Table I. Results of SIMPER analysis. Species were ranked according to their average contribution to similarity between assemblages in the Ría de Ares-Betanzos. Average abundance, ratio value (similarity/standard deviation, Sim./SD), and percentage of cumulative similarity were also included.
Tabla I. Resultados del análisis Simper. Los rangos de las especies están organizados de acuerdo con la contribución a la similaridad entre los grupos de estaciones en la Ría de Ares-Betanzos. Se incluye la abundancia media, valor del 'ratio' (similaridad/desviación estándar, Sim./SD), y el porcentaje de la similaridad acumulada.

Group 1 (average simil.: 26.01%)	Av.Abund.	Av.Sim.	Sim./SD	Contrib.%	Cum.%
Goodallia triangularis (Montagu, 1803)	28.53	7.78	0.88	29.92	29.92
Clausinella fasciata (da Costa, 1778)	13.87	7.40	1.00	28.44	58.36
Gari tellinella (Lamarck, 1818)	3.87	2.91	0.71	11.19	69.55
Spisula elliptica (Brown, 1827)	0.73	0.95	0.35	3.65	73.20
Timoclea ovata (Pennant, 1777)	6.33	0.80	0.28	3.06	76.26
Tellina donacina Linné, 1758	2.13	0.77	0.29	2.98	79.24
Retusa mammillata (Philippi, 1836)	1.07	0.74	0.28	2.84	82.07
Caecum trachea (Kanmacher, 1798)	12.73	0.60	0.27	2.32	84.40
Caecum glabrum (Montagu, 1803)	4.00	0.56	0.27	2.14	86.54
Euspira pulchella (Risso, 1826)	0.40	0.51	0.29	1.96	88.50
Obtusella intersecta (Wood, 1857)	1.73	0.48	0.22	1.86	90.36
Group 3 (average simil.: 28.74%)	Av.Abund.	Av.Sim.	Sim./SD	Contrib.%	Cum.%
Chamelea striatula (da Costa, 1778)	21.33	13.01	1.34	45.27	45.27
Nassarius reticulatus (Linné, 1758)	15.50	8.13	2.04	28.30	73.56
Thracia papyracea (Poli, 1791)	7.50	1.65	0.37	5.74	79.30
Tellina fabula Gmelin, 1791	3.50	1.44	0.46	5.01	84.31
Mysella bidentata (Montagu, 1803)	3.17	1.37	0.53	4.78	89.09
Turbonilla acuta (Donovan, 1804)	9.50	0.94	0.32	3.26	92.35
Group 4A (average simil.: 43.38%)	Av.Abund.	Av.Sim.	Sim./SD	Contrib.%	Cum.%
Ringicula auriculata (Ménard, 1811)	49.10	12.76	1.59	29.42	29.42
Pandora inaequivalvis (Linné, 1758)	32.80	11.56	2.22	26.65	56.07
Nassarius reticulatus (Linné, 1758)	5.00	3.46	1.01	7.98	64.04
Chamelea striatula (da Costa, 1778)	12.80	3.37	0.66	7.78	71.82
Mactra stultorum (Linné, 1758)	2.40	2.61	1.18	6.01	77.84
Turbonilla acuta (Donovan, 1804)	3.70	2.03	0.75	4.68	82.51
Spisula subtruncata (da Costa, 1778)	3.80	1.96	0.69	4.51	87.02
Nassarius pygmaeus (Lamarck, 1822)	11.40	1.37	0.37	3.15	90.17
Group 4B (average simil.: 44.86%)	Av.Abund.	Av.Sim.	Sim./SD	Contrib.%	Cum.%
Nassarius pygmaeus (Lamarck, 1822)	34.58	5.98	1.27	13.33	13.33
Nassarius reticulatus (Linné, 1758)	26.58	5.18	2.43	11.55	24.88
Nucula nitidosa Winckworth, 1930	16.25	4.61	2.81	10.28	35.16
Chamelea striatula (da Costa, 1778)	15.83	3.94	1.33	8.77	43.94
Dentalium novemcostatum Lamarck, 1818	30.92	3.07	0.94	6.85	50.79
Ringicula auriculata (Ménard, 1811)	9.83	2.82	1.58	6.30	57.08
Corbula gibba (Olivi, 1792)	18.75	2.73	1.14	6.09	63.17
Pandora inaequivalvis (Linné, 1758)	8.42	2.21	0.89	4.92	68.09
Montacuta phascolionis Dautzenberg & Fisher, 1925	9.83	1.65	0.88	3.68	71.77
Odostomia unidentata (Montagu, 1803)	14.50	1.54	1.05	3.42	75.20
Chrysallida indistincta (Montagu, 1808)	10.58	1.46	0.92	3.26	78.46
Philine aperta (Linné, 1767)	6.42	1.32	0.70	2.94	81.40
Volvulella acuminata (Bruguiére, 1792)	3.33	1.28	1.25	2.85	84.25
Acanthocardia paucicostata (Sowerby, 1841)	10.58	1.22	0.94	2.72	86.97
Thyasira flexuosa (Montagu, 1803)	4.92	0.66	0.60	1.47	88.44
Ondina diaphana (Jeffreys, 1848)	3.58	0.62	0.63	1.39	89.83
Abra alba (Wood, 1802)	3.67	0.60	0.58	1.34	91.17

Table II. Best combinations of variables obtained through BIO-ENV analysis according the values of the Spearman's rank correlation (*p*w) for the Ría de Ares-Betanzos. GR, gravel; CS, coarse sand; FS, fine sand; Q50, median grain size; C/N, Carbon-Nitrogen ratio.
Tabla II. Mejores combinaciones de variables obtenidas a través del análisis BIO-ENV de acuerdo con los valores del coeficiente de correlación de rango de Spearman (pw) para la Ría de Ares-Betanzos. GR, grava; CS, arena gruesa; FS, arena fina; Q50, mediana del tamaño de grano; C/N, relación Carbono-Nitrógeno.

Number of variables	Correlation (pw)	Best variable combination
2	0.508	Depth-FS
3	0.511	Depth-GR-FS
4	0.518	Depth-GR-FS-Silt/Clay
	0.515	Depth-Q_{50}-GR-FS
5	0.516	Depth-Q_{50}-GR-FS-Silt/Clay
	0.516	Depth-GR-CS-FS-Silt/Clay
	0.514	Depth-C/N-CS-FS-Silt/Clay
6	0.516	Depth-Q_{50}-GR-CS-FS-Silt/Clay
	0.515	Depth-C/N-GR-CS-FS-Silt/Clay
	0.512	Depth-Q_{50}-C/N-GR-FS-Silt/Clay
	All 13 variables: 0.410	

Table III. Summary of canonical correspondence analysis (CCA) for the Ría de Ares-Betanzos.
Tabla III. Resumen del análisis de correspondencias canónicas (CCA) para la Ría de Ares-Betanzos.

Axes	I	II	III	IV	Total inertia
Eigenvalues	0.701	0.274	0.212	0.167	5.784
Species-environment correlations	0.927	0.869	0.824	0.883	
Cumulative percentage variance					
of species data	12.1	16.8	20.5	23.4	
of species-environment relation	34.4	47.9	58.3	66.5	
Sum of all unconstrained eigenvalues					5.784
Sum of all canonical eigenvalues					2.035

forward selection of CCA selected depth and gravel as the variables explaining most of the variance in the species data ($p<0.01$), while fine sand and median grain size were found significant only at the 5% level. Axes I and II accumulate 16.8% of the species variance and 47.9% of species-environment variance (Table III). Depth, median grain size, fine sand and silt/clay showed the highest correlations with axis I; correlations with the other axes were less significant. Sampling stations appeared distributed from the right to the left of axis I following an increase in content of fine sand and silt/clay and a decrease in depth and median grain size (Fig. 4). The same pattern can be observed in the MDS ordination with superimposed values of depth, gravel, fine sand and silt/clay (Fig. 5). Thus, the different analyses suggested that distribution of fauna in the study area is mainly related to a depth and grain size gradient.

Description of assemblages: Distribution in the Ría de Ares-Betanzos of the mollusc assemblages determined by multivariate analyses are shown in

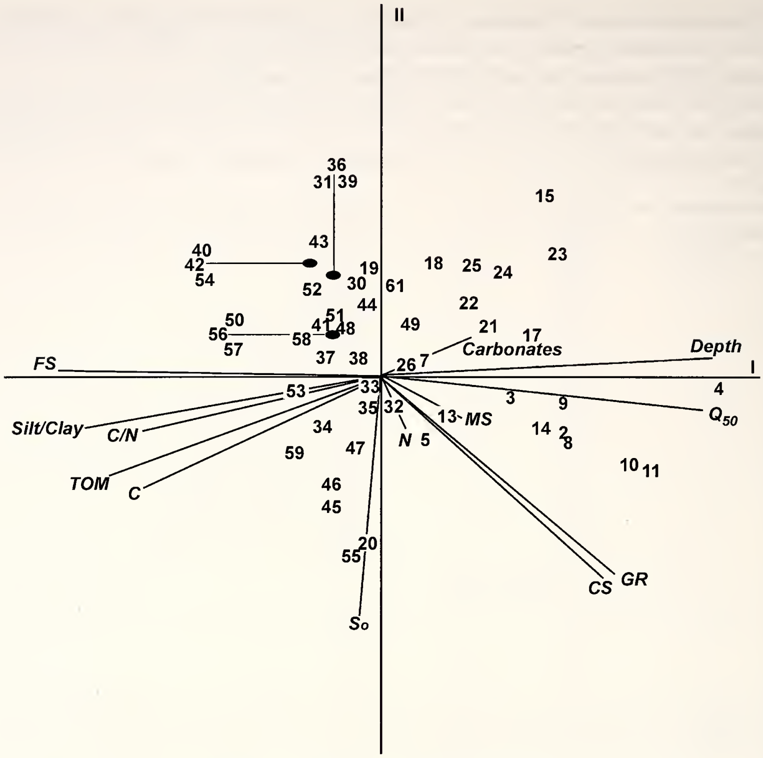

Figure 4. Canonical correspondence analysis (CCA) ordination of stations and environmental variables relative to axes I and II for the Ría de Ares-Betanzos. GR, gravel; CS, coarse sand; MS, medium sand; FS, fine sand; Q50, median grain size; So, sorting coefficient; TOM, total organic matter; C, organic carbon; N, nitrogen; C/N, Carbon-Nitrogen ratio.

Figura 4. Ordenación de las estaciones de muestreo y variables ambientales de la Ría de Ares-Betanzos para los ejes I y II del análisis de correspondencias canónicas (CCA). GR, grava; CS, arena gruesa; MS, arena media; FS, arena fina; Q50, mediana del tamaño de grano; So, coeficiente de selección; TOM, materia orgánica total; C, carbono orgánico; N, nitrógeno; C/N, relación Carbono-Nitrógeno.

Figure 6 and their environmental and faunistic characteristics in Table IV.

Group 1 is comprised of the deepest bottoms of the ría; sediments are mostly composed of coarse sand, medium sand and gravel with a high carbonate content. The assemblage is numerically dominated by *Goodallia triangularis*, *Caecum trachea* (Kanmacher, 1798) and *Clausinella fasciata*; other characteristic species were *Gari tellinella*, *Timoclea ovata* (Pennant, 1777) and *Caecum glabrum* (Montagu, 1803), which are distributed almost exclusively in these bottoms.

In Group 3, sediment are composed of fine sand and median sand and has a higher amount of silt/clay and carbonate content than group 1. The species composition of these bottoms indicates a transition between the fauna of coarser sediments (group 1) and muddy sand/muds (groups 4A, 4B). This assemblage is characterized by a high abundance of *Chamelea striatula*, *Nassarius reticulatus* and *Turbonilla acuta* (Donovan, 1804) and by the presence of *Thracia papyracea* and *Mysella bidentata*. Mollusc abundance per station is lower than in coarse sands and total species number is greater (49 vs 38). The MDS ordination showed that stations 22 and 61 have certain affinities with this

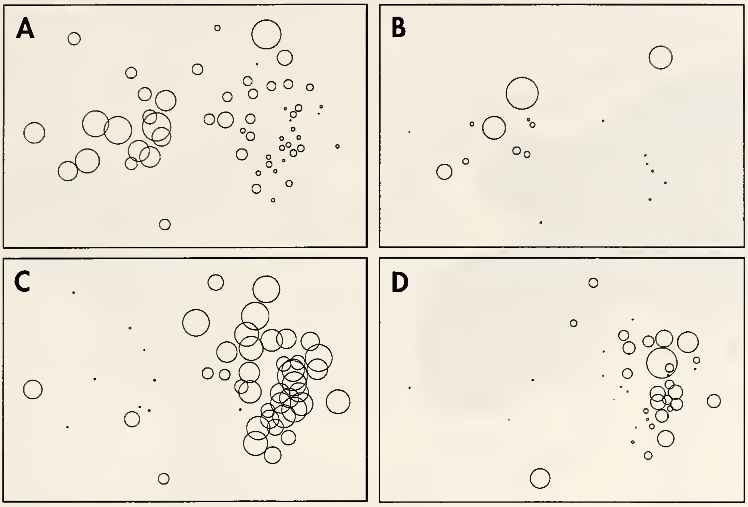

Figure 5. Non-metric multidimensional scaling (MDS) ordination of mollusc assemblages in the Ría de Ares-Betanzos with superimposed values of the abiotic variables selected by BIO-ENV analysis. A: depth; B: gravel; C: fine sand; D: silt/clay. Circle size is proportional to values of variables in each sampling station.

Figura 5. Ordenación MDS de las asociaciones malacológicas en la Ría de Ares-Betanzos con los valores superpuestos de las variables abióticas seleccionadas por el análisis BIO-ENV. A: profundidad; B: grava; C: arena fina; D: limos/arcillas. El tamaño de los círculos es proporcional al valor de las variables en cada estación de muestreo.

assemblage, although the presence of *Tellina fabula* Gmelin, 1791 and *Donax trunculus* also suggest a mix with the faunal assemblage from intertidal sediments.

Group 4A is spread in shallower bottoms which have a greater fine sand and silt/clay content. Total abundance and species number per station are higher than in the previous groups. The dominant species are *Ringicula auriculata* and *Pandora inaequivalvis*, and several species, such as *Chamelea striatula* and *Nassarius reticulatus*, were shared with group 3 although in lower abundances and with a more irregular presence. On the other hand, the bivalves *Mactra stultorum* and *Spisula subtruncata* were mostly found in this assemblage.

Sediments in group 4B are slightly muddier than those of group 4A and have a greater organic content. Dominant species in terms of abundance were *Nassarius pygmaeus*, *Dentalium novemcostatum* and *Nucula nitidosa*; other characteristics species were *Corbula gibba*, *Nassarius reticulatus*, *Acanthocardia paucicostata*, *Chamelea striatula*, *Ringicula auriculata* and *Pandora inaequivalvis*, although the latter two were less abundant than in group 4A.

DISCUSSION

According to our analyses, the distribution of the molluscan fauna in the Ría de Ares-Betanzos seems to be primarily determined by gradients in depth and grain size. The latter was characterized by an increase in fine sand and silt/clay content from the mouth of the ría towards the inner margins. This sedimentary gradient is related to tidal current systems and interactions between oceanic and continental water (SÁNCHEZ-MATA *ET AL.*, 1999). The presence of coarser sediments in the mouth is due to a stronger hidrodynamism (TRONCOSO *ET AL.*, 1993) while a deposi-

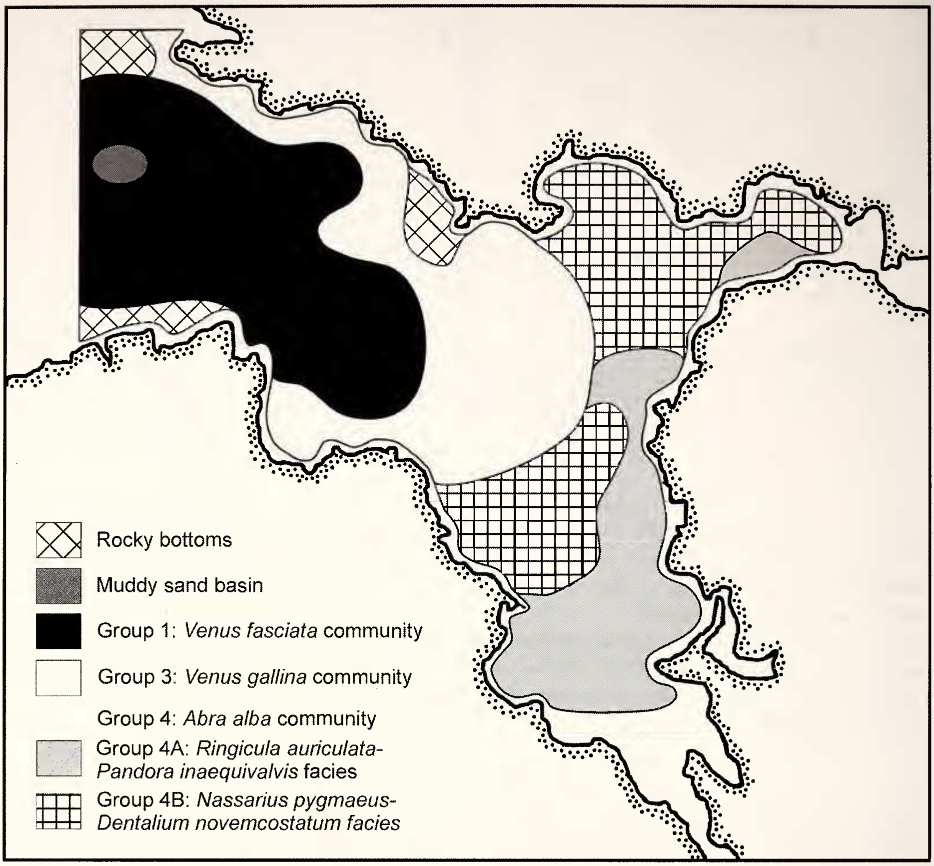

Figure 6. Spatial distribution of mollusc assemblages in the Ría de Ares-Betanzos as determined through cluster analysis.
Figura 6. Distribución espacial de las asociaciones malacológicas en la Ría de Ares-Betanzos determinadas por el análisis cluster.

tion of finer fractions occurs in inner, sheltered areas. This relationship of depth and sedimentary composition with faunal distribution was also observed by a large number of authors (RHOADS AND YOUNG, 1970; GRAY, 1974; EVANS AND TALLMARK, 1976; GLÉMAREC, 1978; TUNBERG, 1981).

According to their faunistic composition and environmental features, the mollusc assemblages in the Ría de Ares-Betanzos could be defined using the classic terms of 'community' and 'facies' (PETERSEN, 1918; THORSON, 1957). Thus, group 1 has a fauna that could be included among the different varieties of the '*Branchiostoma lanceolatum-Venus fasciata* community' (THORSON, 1957). Several authors have reported the presence of similar faunal associations in other areas of Galicia such as Ría da Coruña (LÓPEZ-JAMAR AND MEJUTO, 1985) and Ensenada de Baiona (MOREIRA, QUINTAS AND TRONCOSO, 2005). These bottoms have clean coarse sediments with a high content of biogenic carbonates and are located at the outer areas of the rías where the hydrodynamism is stronger (NOMBELA, VILAS, RODRÍGUEZ AND ARES, 1987). The fauna present in group 3 agrees with the description of the '*Venus gallina* commu-

Table IV. Summary of biotic and physical characteristics of the four molluscan assemblages in the Ría de Ares-Betanzos determined through cluster analyses (values: mean ± standard deviation). Dominant species in any given assemblage are those which account for ≥75% of total abundance.
Tabla IV. Resumen de las características bióticas y físicas de las cuatro asociaciones malacológicas de la Ría de Ares-Betanzos determinadas a traves del análisis cluster (valores: media ± desviación estándar). Las especies consideradas como dominantes en cada una de las asociaciones fueron áquellas que representaron ≥75% de la abundancia total.

	Group 1	Group 3	Group 4A	Group 4B
Dominant species	*Goodallia triangularis* *Clausinella fasciata* *Caecum trachea* *Timoclea ovata*	*Chamelea striatula* *Nassarius reticulatus* *Turbonilla acuta* *Thracia papyracea* *Chrysallida decussata*	*Ringicula auriculata* *Pandora inaequivalvis* *Chamelea striatula* *Nassarius pygmaeus*	*Nassarius pygmaeus* *Dentalium novencostatum* *Nassarius reticulatus* *Corbula gibba* *Nucula nitidosa* *Chamelea striatula* *Odostomia unidentata* *Calyptraea chinensis* *Acanthocardia paucicostata* *Chrysallida indistincta* *Ringicula auriculata* *Montacuta phascolionis*
N	89.93±87.65	79.67±53.61	172.22±114.38	286.50±179.15
S	8.86±5.08	8.67±3.70	12.44±3.68	22.92±6.89
Depth	27.35±8.33	13.21±2.58	5.78±3.10	7.21±2.30
% Gravel	18.29±23.63	1.25±2.56	0.07±0.10	1.85±2.14
% Coarse sand	52.04±25.62	9.12±16.16	2.29±2.59	7.33±8.17
% Medium sand	18.76±19.65	20.39±16.16	9.84±14.77	10.09±8.17
% Fine sand	10.51±18.33	60.53±17.82	73.20±15.70	64.78±11.68
% Silt/Clay	0.39±0.60	8.71±7.91	14.60±11.11	15.96±8.76
Q_{50} (mm)	0.87±0.59	0.17±0.07	0.13±0.05	0.14±0.05
Sedimentary type	Coarse/medium sand	Fine/muddy sand	Fine/muddy sand	Muddy sand/Sandy mud
% TOM	0.14±0.19	0.44±0.18	0.86±0.48	1.13±0.77
% Carbonates	38.47±21.92	40.49±8.66	29.50±6.48	28.15±13.7

nity' (THORSON, 1957), corresponding to the fine sand bottoms of the center and northern outer margin of the ría in which the bivalve *Chamelea striatula* and the gastropod *Nassarius reticulatus* show their greater abundance. Both species are also spread in shallower finer sandy bottoms although in lower abundances.

Even though group 4 have some species typical of the '*Venus gallina* community' such as *Chamelea striatula* and *Mactra stultorum*, there is an important presence of several other species which show preference for muddier sediments (*Corbula gibba, Thyasira flexuosa, Nucula nitidosa*). Thus, this group could be considered as a mix between the already mentioned community and the '*Syndosmia* (=*Abra*) *alba* community' of PETERSEN (1918). This situation agrees with the results showed by Sánchez-MATA AND MORA (1999b) for all groups of macrofauna in the Ares sector of the ría. On the other hand, the '*Abra alba* community' has been reported along European coasts in different types of muddy bottoms (REES AND WALKER, 1983; GENTIL, IRLINGER, ELKAIM AND PRONIEWSKI, 1986; LASTRA, MORA, SÁNCHEZ AND TRONCOSO, 1988) as well as in Galician rías (Cadée, 1968; Olabarría, Urgorri and Troncoso, 1998; Sánchez-Mata and Mora, 1999b; Moreira *et al.*, 2005). However, multivariate analyses have distinguished two further groups within group 4, which can be characterized as two different malacological 'facies'. The facies corresponding to group 4A is determined by the dominance of *Ringicula auriculata* and *Pandora inaequivalvis*, and that present in group 4B is characterized by *Nassarius pygmaeus* and *Dentalium novemcostatum* and shows a greater presence of species preferring muddier sediments. Several authors have suggested that the different proportion of sand and silt/clay is a major factor in structuring benthic communities (Rhoads and Young, 1970; Gray, 1974). Webb (1969) pointed out that even a small silt/clay content affects the sediment porosity and therefore the faunal composition. In the Ría de Ares-Betanzos, the variations in amount of fine sand and silt/clay seems to condition mollusc species abundance across these bottoms and consequently the presence of any given facies.

In general, mollusc distribution in sandy sediments of the outer and central part of the ría is similar to those observed in Ría de Coruña (López-Jamar and Mejuto, 1985) and Ensenada de Baiona (Moreira *et al.*, 2005). The transition between the '*Venus gallina*' and the '*Abra alba*' communities occurring in the inner areas of the Ría de Ares-Betanzos has been also reported for several Galician Rías (López-Jamar, 1981; Sánchez-Mata and Mora, 1999b). Although multivariate analyses were able to distinguish the two described facies in finer sediments in the Ría de Ares-Betanzos, there are several abundant species which are widespread, such as *Chamelea striatula, Nassarius reticulatus, Pandora inaequivalvis* and *Ringicula auriculata*. This situation agrees with the '*continuum*' concept which implies that species are independently distributed along environmental gradients (Curtis, 1955). Thus, co-existence or overlap between them in any given assemblage would be related to their reactions to the existing gradients (Mackie, Oliver and Rees, 1995). In our case, variations in abundance of any given mollusc species across the different assemblages in Ría de Ares-Betanzos would be conditioned by a depth-grain size gradient.

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